1840. *O. montana*, Blyth, Proc. Zool. Soc. 1840, p. 77.
1840. *O. californiana*, Blyth, *ibid.*
1851. *O. montana*, Audubon and Bachman (fig.).
1854. *O. montana*, Richardson, Voyage of H.M.S. 'Herald' (osteological fig.).
1857. *O. montana*, Baird, Mammals N. America, Survey Reports, p. 673 (fig. of horn).
1859. *O. montana*, Schott, U. S. Mexican Boundary Report, part ii. p. 52.
1871. *O. canadensis*, Blyth ("Zoophilus"), The Field, May 13 (fig.).
1880. *O. cervina*, Alston, Biologia Centr.-Am., Mammal. p. 111.
1884. *O. montana dalli*, Nelson, Proceedings of U. S. National Museum, vol. vii. p. 13.

9. On the Avian Sternum.

By Beatrice Lindsay, Girton College, Cambridge [1].

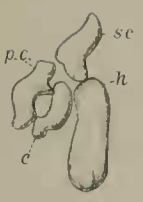
[Received June 16, 1885.]

(Plates XLII.–XLV.)

Introduction.

The most typical and simple form of the sternum is that found in Reptiles, where this bone, although associated with a shoulder-girdle of maximum complexity, and strengthened by the apposition of an interclavicle in the median line, is itself undoubtedly of homogeneous origin, that is to say derived solely from the fusion of ribs. In Birds and Mammals the sternum has been supposed by some authorities to be, on the contrary, a composite structure, containing a supplementary median element more or less distantly derived from membrane-bone, and homologous with the free T-shaped interclavicle of Reptiles. Much has been done to increase the plausibility of that theory by a vague use of the terms "interclavicle" and "episternum." These names, when first introduced, expressed nothing but a certain anatomical position of the parts to which they were applied; but now that the aforenamed reptilian structure is held by nearly all anatomists to be a membrane-bone, the names given to it inevitably tend to suggest a meaning restricted to particular homologies. But, unfortunately, many authors still apply the said names indiscriminately to any anterior median ossification, or paired ossification approaching the median line, without regard to its origin, whether known or unknown; and thus they unintentionally create factitious evidence for the above-named theory, by the continual implication of homologies which have never been satisfactorily proved. Instances in point are afforded by certain

[1] Communicated by Dr. H. Gadow, C.M.Z.S.



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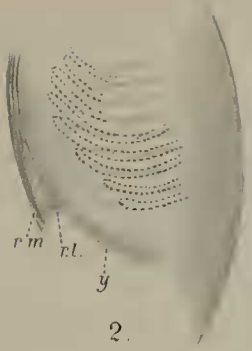

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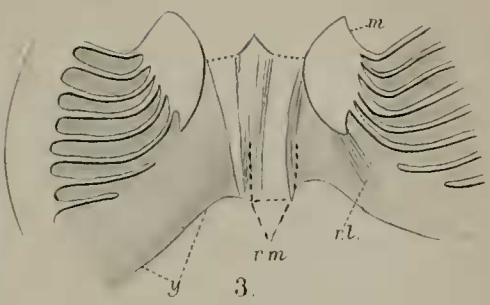

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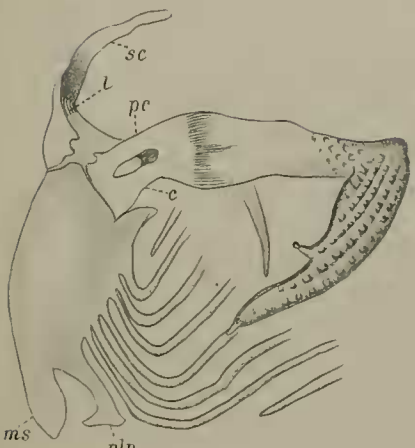

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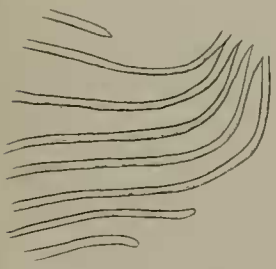

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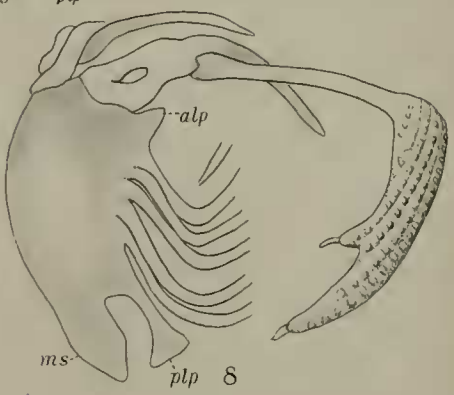

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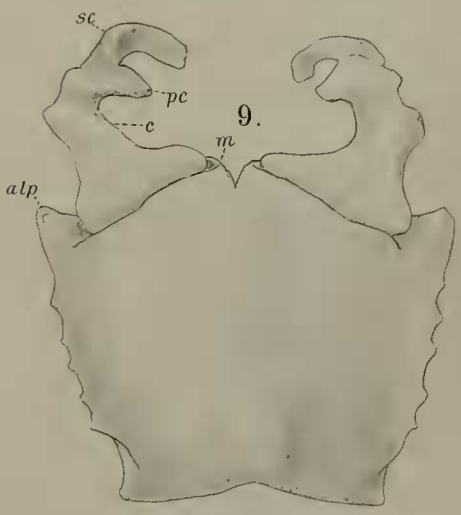

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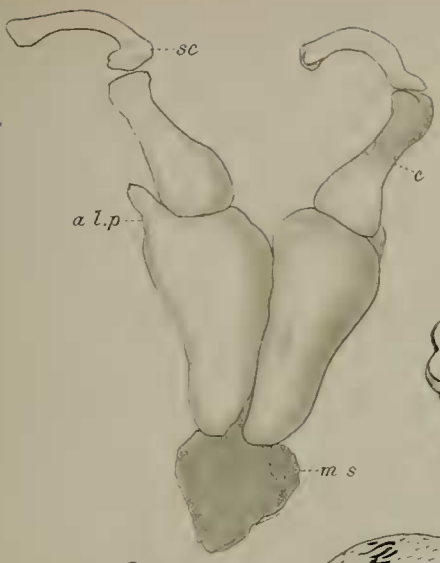

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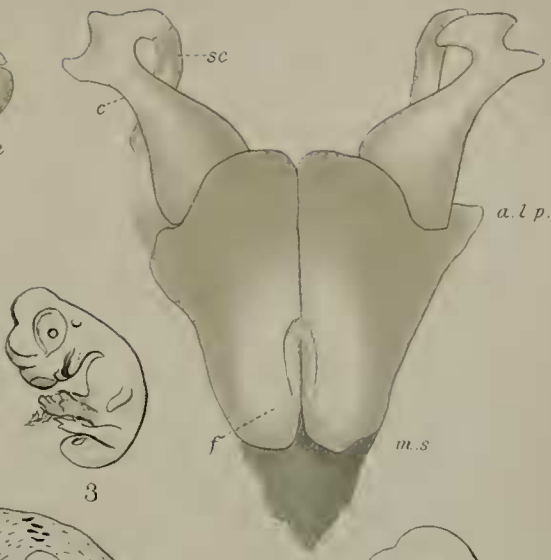

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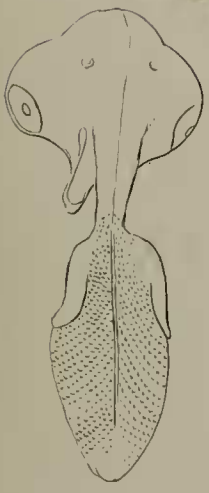

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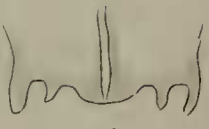

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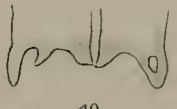

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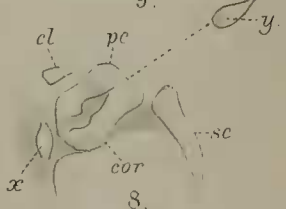

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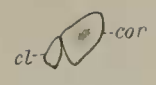

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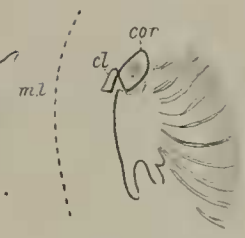

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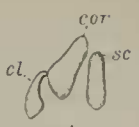

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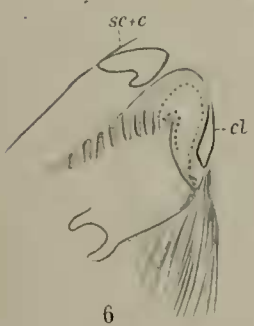

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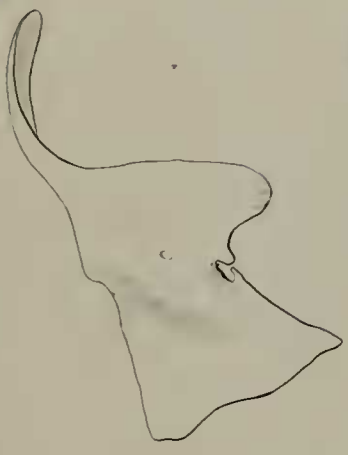

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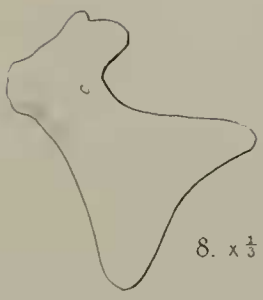

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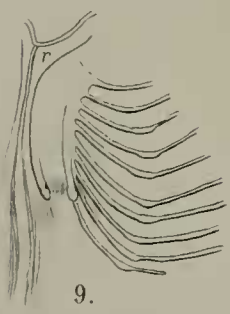

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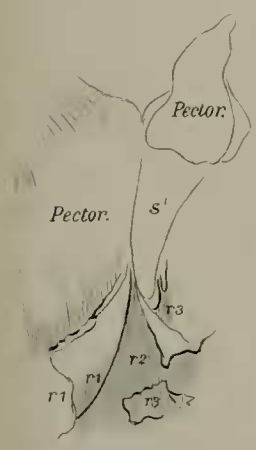

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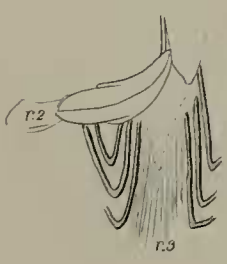

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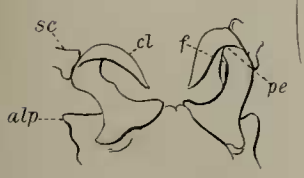

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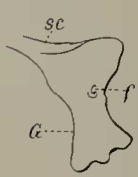

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occasional centres of ossification in the human sternum, and by the median apophysis of the avian furcula.

So far as regards the sternum of the higher Mammalia, the balance of recent evidence is certainly not in favour of the theory under consideration. The costal origin of the manubrium sterni is asserted by Ruge on the ground of embryological evidence; while the complexity of its centres of ossification, so fully discussed by Prof. Albrecht in his recent paper on the human sternum, points to an origin from the fusion of many serial members, rather than from the differentiation of an interclavicle—a process, it may be added, which could have had no *raison d'être* in a bone placed under conditions involving comparatively little mechanical strain. With regard to the avian sternum, on the contrary, no recent evidence has been offered in opposition to the theory maintained by Götte and Hoffmann, which asserts the presence of an interclavicular element united with the costal sternum, and forming the crista sterni or keel[1]. This theory will be examined from a critical point of view in the following communication, the object of which is to discuss the origin of the avian sternum and its various parts.

The communication consists of three sections, arranged in the following order:—

PART I. (i.) Statement of the chief views held as to the nature of the Avian Sternum, and of the nomenclature of its parts adopted by the best authorities, where this offers any special peculiarity; (ii.) Comments on certain of the above views.

PART II. Details of the embryonic development of the sternum and adjacent parts in five types of bird (with Plates).

PART III. Summary of the conclusions apparently suggested by the latter, in connection with previously recorded facts.

[1] It should be added at the outset that no conclusion can be gained from the consideration of other types than birds; for while on the one hand we may refer to the keel of the sternum in Bats, which is admittedly the outgrowth of the sternum itself, belonging both to the presternum and mesosternum, yet on the other hand we must admit the existence in *Hatteria* of a keel formed by coalescence of the interclavicle with the sternum, and affording attachment to the pectoral muscles (see "Contributions to the Anatomy of *Hatteria*, or *Rhynchocephalus* of Owen," by A. Günther, M.A., Ph.D.: Phil. Trans. 1867, p. 595).

Part I.—(i.) Tabular Statement of the Theories held, *Facts adduced, and Nomenclature adopted by various Writers with regard to the* Avian Sternum.

Details are added with regard to such parts of the shoulder-girdle and its ligament as have been supposed to afford evidence with regard to the composition of the Sternum.

Theory.	Evidence adduced in support of Theory, and Nomenclature of Parts of Sternum, etc.
1. L'Herminier's view (date 1830).—That the Avian sternum consists typically of 9 ossifications in 3 rows.	*Evidence.*—Investigation of the ossifying sternum. *Nomenclature.*—The anterior row of centres of ossification consists of three parts—a median *prosternum* and two *prosternals*, constituting the *prosternum*. The intermediate row consists similarly of *mesosternum* and two *mesosternals*, constituting the *mesosternum*; and the posterior row of *metasternum* and two *metasternals*, constituting the *metasternum*. The centres which occur most frequently are the mesosternals, and in the Ostrich these alone exist.
2. C. G. Carus's view (date 1834).—That the middle portion of the episternum of Saurians is the equivalent of the crista sterni of Birds.	
3. Rathke's view (date 1853).—That in all types the sternum is costal in origin, while the development of the episternal ligament which unites it with the clavicles is perfectly independent.	*Evidence.*—Results of embryological investigation.
4. Harting's view (date 1864).—That the interclavicle is represented in Birds (both Ratitæ and Carinatæ) by the system of ligaments between sternum, coracoid, and clavicle, together with the processes to which they are attached.	*Evidence.*—Anatomical position in the adult of the system of ligaments described, together with that of the processes which frequently afford attachment to those ligaments, and occasional pathological ossifications in the ligaments themselves. *Nomenclature.*—Three parts of the said system of ligaments are distinguished, namely:—(i) *vertical median posterior* lamina of ligament; (ii) *vertical median* or *sterno-clavicular* ligament; and (iii) *lateral superior* paired lamina, or *coraco-clavicular* ligament. (i) and (ii) are included under Götte's "sterno-clavicular ligament," the distinction between them being that (i) has a lateral, and (ii) an anterio-posterior extension.

5. Parker's view (date 1868).—That our present knowledge of the sternum does not justify any complete interpretation of the morphological value of its parts; that nevertheless the "lophosteon" may be regarded as a feature of Avian rather than pre-Avian date; and that the division of the sternum by fontanels or notches is due to a process of absorption, while their position marks the boundary of definite and important ossifications.

Evidence.—Comparison of adult forms and late stages of the young, for the most part after commencement of ossification.

Nomenclature.—The sternum has three typical divisions in longitudinal succession, the *Prosternal*, *Mesosternal*, and *Xiphisternal*. The first is ossified by a paired centre called the *Proosteon* (existing in *Rhea*, &c.), the second by a paired *Pleurosteon*, and the third by the *Urosteon*, existing in rare cases (*Dicholophus*, e. g.).

There also exists a less important division into three regions in transverse succession, viz. the *lateral* region, paired, the *intermediate* region, paired, and the *mesial*, which, though really paired, is apparently single. The last is ossified by a centre called the *Lophosteon*, corresponding with the keel.

Besides the typical *Proosteon*, *Pleurosteon*, and *Lophosteon*, and the rare *Urosteon*, there are other centres of ossification, viz., the *Metosteon*, paired, existing behind the Pleurosteon in Crows and Gallinacea; and the *Coracosteon*, present on each side of the Lophosteon in *Turnix*.

Of these the *Lophosteon*, *Urosteon*, and *Coracosteon* are centres solely ornithic; while the *Pleurosteon* is found paired in Reptiles, the *Metosteon* corresponds with the partial ossification of the posterior-lateral process in *Stellio* and *Iguana*, and the *Proosteon* is found in certain Mammals, either paired or single.

The typical posterior processes of the sternum as seen in the Pheasant are named the *External Xiphoid*, *Intermediate Xiphoid*, and *Middle Xiphoid*. The last lies posterior to the keel, and has also been termed the *Entosternum* or *the middle xiphisternal process*.

(*Note.*—The Pleurosteon is thus the equivalent of L'Herminier's lateral mesosternals, and the representative of the primitive costal halves of the sternum.

The Proosteon, as existing in *Rhea*, I suppose to be the ossification of the anterior lateral process, whereof the gradual addition is traced in the Ostrich. Where it is absent, I imagine that this process is simply a degraded portion of the anterior part of the costal sternum. This view I derive from its condition in the chick, where this process, although in the adult it looks like a secondary addition, is ossified by the Pleurosteon, and has a primitive connection with anterior ribs, in the early embryo.)

Tabular Statement (*continued*).

Theory.	Evidence adduced in support of Theory, and Nomenclature of Parts of Sternum, etc.
6. Huxley's view (date 1871, 'Anatomy of Vertebrated Animals,' pp. 240, 248).—That the interclavicle is represented by the median part of the furcula, but that its occasional elongation into a process is a secondary addition, while the secondary character of its rare union with the keel is suggested by comparison of the union of the coracoid and clavicles in *Didus* and *Opisthocomus*; that the keel is quite independent of the interclavicle, and that the posterior processes of the sternum are formed in consequence of imperfect ossification, and are comparable with the division of the xiphoid process of Mammalia.	*Evidence.*—Comparison of adult forms and late stages of the young, after the commencement of ossification. *Nomenclature.*—The occasional anterior median process of the sternum is called the *rostrum* or *manubrium*, but no more important character than that of a mere outgrowth is claimed for it. The occasional median process of the "interclavicle" is called the *hypocleidium*, while the anterior lateral angles of the sternum, including part of the region which affords attachment to ribs, are called the *costal processes*. The rest of the nomenclature adopted is that of Prof. Parker.
7. Gegenbaur's views: (i.) (Date 1859).—That the costal sternum of Birds is supplemented by an element homologous with the Reptilian interclavicle, which forms the keel. This earlier view, which suggested the direction of Götte's researches, was afterwards abandoned. (ii.) (Date 1877, Elements of Comp. Anat. 2nd ed. Bell's transl., pp. 442, 443, 444).—That the keel is a process of the sternum, physiologically corresponding with that found in "aerial mammals," while the episternum is wholly absent; that the posterior processes are formed by the occurrence of fontanels; and that, as compared with the sternum of Reptiles, the sternum of Birds has suffered a diminution of its posterior length, this being indicated by the relatively small number of ribs attached to it.	
8. Götte's view (date 1877).—The same as Gegenbaur's earlier view; also that the *sterno-clavicular* ligament forms an integral part of the interclavicular structure; further, that the keel + ligament is also homologous with the mammalian manubrium sterni.	*Evidence.*—Results of embryological investigations on chicks of 4 to 5 days' incubation, and on the conditions of commencing ossification in the median part of the furcula of chicks of 8 days' incubation.
9. Hoffmann's view (date 1879).—The same as Götte's, regarding the nature of the keel.	*Evidence.*—Results of investigations as to the nature of the cartilaginous keel in several embryos, and of the sterno-clavicular ligament in young birds of several types.

The foregoing summary of theory with regard to the Avian Sternum would be incomplete without reference to the recent researches on the Mammalian Sternum which have been already mentioned, namely those of Ruge, which established the costal origin of the *xiphisternum* of man; and those of Albrecht, which have lately added more force to Ruge's conclusions as to the costal origin of the *manubrium sterni*. The result in the former case precludes us from admitting that the posterior processes of the avian sternum are, as suggested by Huxley, homologous with the xiphisternum of man[1]; and in both it greatly weakens the argument for the interclavicular homology of the keel, while at the same time it points out a line of research with regard to the anterior region of the avian sternum, which has been followed during the investigation hereafter described.

(ii.) Certain of the theories named call for some comment. Firstly, with regard to that of L'Herminier, it is obvious that at the date of his researches the phylogenetic value of anatomical features was but little understood; we are therefore not bound to accept L'Herminier's own estimation of the equal value of his three typical rows of ossific centres with the confidence which at first sight might seem due to his numerous facts and clear description of them. Nevertheless his record of the respective dates at which the various centres appear affords a valuable clue to the order of development of the respective parts, the details of which will be discussed hereafter.

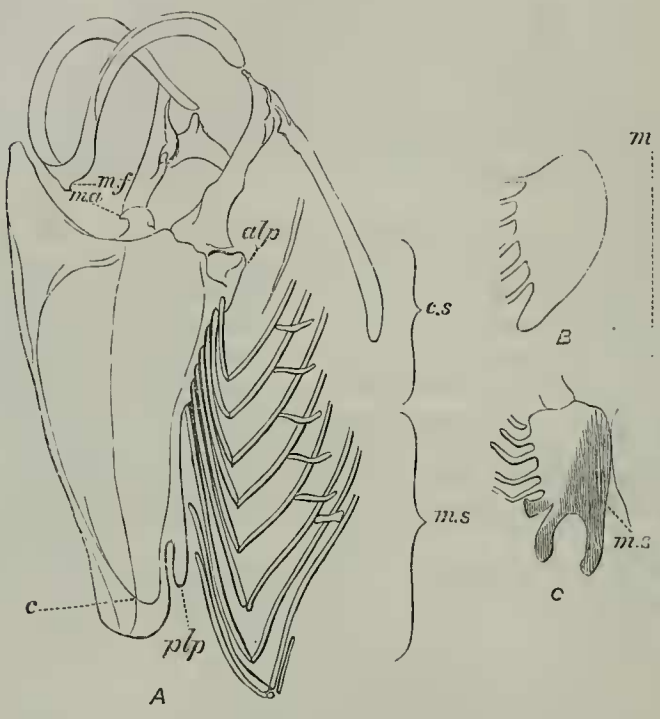
Secondly, with regard to Harting's theory, several objections present themselves at first sight. Were the system of ligaments, with the bony processes which afford them attachment, to be regarded as an "episternum," it would afford a unique case of a bone undergoing degradation at the centre, yet ossifying at odd points in its original periphery. Again, there is no reason to place any especial emphasis on the occurrence of the ossifications indicated, since all ligaments tend to present occasional ossifications. Further, the fact that the ligament system of the Ostrich is claimed as an episternal apparatus in which the clavicles have not been differentiated, amounts to a *reductio ad absurdum* of the theory; for these ligaments, exceedingly thin in the adult, are scarcely possible to find in the embryo, in which, on Harting's hypothesis, we should expect to find them better developed.

It appears, then, that the evidence for the interclavicular homology of the keel must rest on the embryological researches of Götte and Hoffmann. For this reason, further evidence upon the disputed point of the keel has been sought in a series of embryos of five types. All points of interest observed in these embryos are described in the ensuing section, Part II. It is to be noticed, however, that some difficulty occurs in comparing the results obtained with those of the

[1] It is possible, however, that they may be comparable to that of the Jerboa or the Kangaroos, in which animals this process is probably a secondary addition to the costal sternum, or even to the xiphisternum of the Frog, which also is an appendage to a costal sternum, if Ruge's view of the latter be correct.

above-named observers, owing to some discrepancies in their statements as to the age of embryos. Götte describes the establishment of coracoid, clavicle, and sternum in chick embryos of the age of 4–5 days, and yet considers that his embryos were slightly older than

Fig. I.



A. Sternum of adult Guillemot (*Uria troile*). B. Sternum of Ostrich embryo, consisting, before fusion of the lateral halves, of costal sternum only. C. Sternum of Chick embryo, consisting, before fusion, of both costal sternum and metasternum.

c.s, *costal sternum*, extending from the attachment of the coracoid to that of the last sternal rib; *m.s*, *metasternum*, extending posteriorly from the last sternal rib [1]; *m.f*, median furcular apophysis; *m.a*, median anterior sternal apophysis; *a.l.p*, anterior lateral process of the sternum; *p.l.p*, posterior lateral process of the sternum.

Rathke's. These descriptions do not correspond with the usually received opinion that the histological differentiation of the mesoblast takes place during the fifth day of incubation in the chick [2]; still less

[1] This region does not exactly correspond with L'Herminier's metasternum, for that bears some of the posterior ribs, and therefore includes part of the costal sternum.

It corresponds, however, with the region occupied by Parker's Lophosteon + Metosteon + Urosteon, in other words its extent is not only posterior but also median. In short, the term metasternum is used here to express rather its development in time than its position in place.

[2] 'Elements of Embryology,' Foster and Balfour, 2nd ed. p. 270.

do those of Hoffmann, who describes the connection of sternum and clavicle taking place "durch an Knorpelzellen reiches Bindegewebe," in sections of *Carbo cormoranus* "von zwei Tage alten *Embryonen*." Götte's sections of 4–5 days' chicks probably correspond with those called chicks of 6 days' incubation in the Cambridge Morphological Laboratory. In these, however, I fail to detect the darker tissue which he describes as connecting sternum and clavicle. They correspond with the earliest stages which I have dissected, figured in Plate XLV. figs. 9, 10, 12, 14.

The nomenclature used throughout this paper is explained by Fig. I. p. 690.

Part II. Details of Embryonic Development in five Types, namely (i.) the African Ostrich (*Struthio camelus*), (ii.) the Guillemot (*Uria troile*), (iii.) the Gull (*Larus*), (iv.) the Chick, and (v.) the Gannet (*Sula alba*).

These embryos were not examined in sections, but were dissected; and this for two reasons: first, comparison of stages is easier if one method of preparation is employed throughout; and the younger specimens can be dissected, whereas the older ones, with which it is safest to begin, cannot be made into sections; secondly, sections are useless in studying the development of muscles, which is of necessity intimately connected with that of bones, and may therefore give some clue to their history. A chick in which the pericardial cavity is not yet closed can be dissected with perfect accuracy under a strong lens: indeed dissections can be made at a stage so early that they are useless, since the microscope shows little difference between various cells, and there is no means of checking the results of dissection by the histological character of different parts; this is a consequence of the fact that the first change the differentiating cells undergo is a change in their firmness and closeness. Plate XLIV. figs. 3–5 correspond with the stage called "early 6th day" in the Cambridge Morphological Laboratory, sections of which show comparatively little differentiation in the cells of the future shoulder-girdle.

(i.) The Ostrich.

(7 individuals, embryos respectively of 27, 25, 21, 15, 10, 7, and 4 days' incubation.)

The adult Ostrich still presents certain Reptilian features: to wit, (*a*) the presence of two claws on the 1st and 2nd digits of the wing, while other birds that possess such claws, for example Rhea and the Swan, have only one, and most birds have none; (*b*) the broad coracoid, consisting of two parts separated by a foramen. These facts appeared to render it possible *à priori* that in the embryo traces of the Reptilian interclavicle also might be present, either free or, as suggested by Götte's theory, in the form of a rudimentary keel; for the absence of the interclavicle is not implied in the loss of clavicles, as may be seen from its existence in the Crocodile; but, on investigation,

no trace was found either of interclavicle, clavicle, or keel. Too much stress cannot be laid on the absence of the latter, since the character of the fore limb as a true although degraded wing has frequently led, from a point of view exactly opposite to that of Götte, to the suggestion (founded on no other evidence than the analogy indicated) that the sternum of the Ratitæ has lost a formerly existing keel: this statement must now be directly negatived. The absence of a keel might indeed be inferred, by all who do not share Götte's view as to its origin, from the smallness of the pectoral muscles, the earlier stages of which afford no ground for supposing that they have assumed their present condition by degradation from a carinate type.

It is unfortunate that no observations have been made on the early embryos of *Rhea* or *Casuarius*, or above all on those of *Dromæus*, whose rudimentary clavicles and single sternal plate mark a type singularly different from the other Ratitæ. The Ostrich embryos, however, presented numerous points of interest, given below.

1. In the 4 days' embryo, *scapula and coracoid are not united*; this points to the conclusion that their subsequent union is a secondary rather than an ancestral reptilian condition. Furthermore, the *coracoid and precoracoid are separate*. Götte and Hoffmann both came to the conclusion that the distinction between the two parts arose by the establishment of a foramen in a cartilage originally uniform; the 4 days' embryo shows, however, that the division between them is of different origin. The precoracoid thus exhibits its maximum development in the earliest stage; in the adult it sometimes shows a tendency to atrophy (*cf.* Plate XLII. fig. 9; Bronn figures a similar specimen). In the absence of further evidence this fact would have gone far to justify a belief that the precoracoid was wanting in the shoulder-girdle of other birds, but, as will be seen hereafter, there are reasons for a contrary opinion.

2. The rectus abdominis muscle is in the 7 days' embryo attached to the unfused sternal halves, passing up between them in the median line, about to the level of the third sternal rib, where they meet one another; the muscle is broad, and its lateral portions exhibit two thick bands which are attached to the sternal halves. In the adult the median portion is attached to the borders of the cartilaginous metasternum, which is apparently developed for its support, while the lateral portions become very thin.

3. In the 4 days' embryo are seen eight thick transverse muscular bands, overlying as many ribs, *i. e.* all except the two anterior free ribs: in the case of the two posterior ribs, these muscles are longer than the ribs; and in the case of the posterior sternal ribs, they do not follow the sharp curve which these make towards the sternum, but pass nearly straight towards the median line, so that they only overlie the ribs during part of their course. Towards the spine they become lost in undifferentiated muscular tissue. These muscles are on no account to be confounded with the muscle-plates as apparent in a four days' *chick*; bands similar to them appear in a *six days' chick*: their position also, as stated, corresponds with that

of he ribs, *i. e.* is not, like that of the muscle-plates, intravertebral. Ths supercostal position it will be seen, however, from comparison with other types, is only a secondary arrangement occurring during part of their course, in consequence of the curvature of the ribs. They represent, in fact, traces of the *intercostales externi* of ribs in their primitive arrangement, before they acquired their present modifications in connection with the sternum.

4. Although the sternum as a whole is greatly lengthened in the course of its development, owing to the appearance of the metasternum, yet its costal portion loses one posterior attached rib ; there are six sternal ribs in the embryo, five in the adult. Further, a seventh rib, although never attached to the sternum, shortens considerably in the course of development, which implies that it was once a sternal rib. The position of the primitive intercostales externi of the two unattached posterior ribs in the four days' embryo, being, as they are, longer than the ribs they accompany, leaves little doubt that both originally entered into the formation of the primitive costal bands.

5. The series of embryos shows the gradual *addition of the anterior lateral process* to the costal sternum.

6. The 7 days' embryo shows an anterior part which may probably be compared to the *manubrium sterni* of mammals. Its extent in front of the first sternal rib, at a stage when none of the parts known to be of secondary origin have as yet been added to the costal sternum, taken in connection with the existence of two anterior spinal ribs of which the second is very long, seems sufficient to prove its costal origin. Further, St. George Mivart [1] records the appearance in the Ostrich of a rudimentary sternal rib, the first of six, which was not attached to the corresponding spinal rib (the 3rd) ; from the number and position of the spinal ribs he describes, namely ten, whereof the two posterior are not attached to the sternum, it appears that this rudiment corresponds with the first sternal rib, fully attached to the corresponding spinal portion, of the seven embryos here described This affords a further reason for supposing that the process of atrophy extended in the above-named specimen to the third spinal rib has taken place already in the case of the first and second.

7. Comparison of the 15 days' embryo with preceding stages shows the *addition of the metasternum* to the costal sternum. Although this region, seen in all subsequent stages of the embryo, is in perfect continuity with the cartilage of the original costal sternum, yet in the adult (as appears in Plate XLII. fig. 9) only a small part of it is ever ossified. In *Rhea* still less of it is ossified, so that the halves of the sternum remain united by cartilage only. Apparently these do not, however, correspond exactly with the primitive halves ; for a fontanel, nearly closed by thinner bone, marks, in some specimens, a boundary corresponding in position with the notch that separates off the posterior lateral process of the Ostrich (*cf.* fig. IV. *f*, p. 710).

[1] "Axial Skeleton of the Ostrich (*Struthio camelus*)," by St. George Mivart, F.R.S.: Trans. Zool. Soc. x. p. 1.

8. *The differentiation of the lateral processes of the metasternum,* which also are not ossified even in the adult, is traced by their connection with the muscles. They are prolongations, established between the ages of seven and ten days in the embryo, of the ends of the primitive halves of the costal sternum, to which the lateral parts of the rectus are attached. In later stages this lateral part of the rectus becomes very thin, and the processes are found to afford attachment in addition to part of the obliquus externus, as is usually the case with the posterior lateral processes of the sternum in the Carinatæ. Coincidently with this change of their muscular relations, the ends of the processes develop between the 15th and 21st days a double outgrowth, resembling the end of the xiphoid process in the Chick, and apparently due in both types to the somewhat lateral direction of the strain exercised by the obliquus externus. The attachment of this muscle becomes rather obscure in late stages, because in the adult its major part is, as stated by Bronn, aponeurotic; I find that it may, however, be still traced to the process in a bird newly hatched.

It appears, then, that in the Ostrich at any rate the posterior lateral processes consist of the ends of the primitive costal bands, preserved and prolonged for the attachment of the lateral part of the rectus, and subsequently modified to afford attachment to the obliquus externus. Their change of use is due to the reduction that takes place, during the establishment of the Avian type, of the rectus, which muscle finds its maximum development in Reptiles. The primitive costal origin of these processes finds a parallel among the Carinatæ in the case of the Gannet: it is interesting, too, to compare them with the costal processes of the sternum in *Iguana,* formed by the fusion of the sternal portions of posterior ribs.

These processes, as existing in the adult, may be considered a part of the metasternum, since the primitive part bears but a small proportion to the later additions.

(ii.) The Guillemot.

(13 specimens, from about 17 days' to 6 days' incubation.)

This type exhibits two marked peculiarities: (*a*) the great development of the keel and median furcular apophysis; (*b*) the elongated condition of the sternum, which in the adult ossifies seven ribs and is very narrow. The former character, since the bird has small wings and flies but little, must be attributed to the necessity for strengthening the fore limbs in swimming; the second seems to be correlated with the general elongation and narrowing of the trunk established in connection with the habit of diving. The embryos dissected exhibited the following points which call for remark:—

1. The union of the clavicles takes place very early; in a 6–7 days' embryo, when the sternal halves are not yet united, they are already closed, and the median furcular apophysis is mapped out in cartilage continuous with the clavicles. The embryos examined were hence unsuitable for inquiry into the origin of the latter structure, but they

gave ample opportunity for investigating the formation of the keel, which attains a maximum development in this bird, and ought therefore to afford a clear interpretation of its origin. Now the keel, according to Götte's theory, is formed by the posterior growth of the clavicles in the median line; this growth ought, then, to be traced in stages subsequent to the one described, in which the clavicles are already united, but in which the median line posterior to them is occupied solely by muscular tissue, underlying the thinnest possible tract of skin. Such, however, is not the case; the median part of the furcula never exhibits any further posterior growth than in the six days' embryo, where it has the same relative extent as in the adult. The sterno-clavicular ligament, too, which in the course of the process of growth supposed should be formed before the more posterior keel, is entirely absent in the 6 days' embryo, but appears in an embryo of about 8–9 days, where the keel is fully formed; moreover, far from exhibiting the retrogression with advancing age necessary *ex hypothesi*, since it is supposed to have taken place in the course of phylogenetic development, this ligament is very fine at first, and augments in strength as it approaches the adult stage. Stages were not obtained which showed the gradual development o the keel as in the Chick.

In consequence of the early closure of the clavicles, which, as stated above, takes place before the sternal halves are fused, the rectus is attached, at this stage, to the *clavicle*, a condition to be contrasted with that which occurs in the Chick (*v. infra*).

2. The rectus, in stages considerably later, presents a remarkable complexity. In the embryo of some 12–16 days it is divided into three parts, described below:—

A. *Outer sheet*, very thin and continuous with the posterior part of the pectoralis major. This condition of the muscles named was observed in several of the Carinate types examined, while in the case of the Chick something similar occurs at a much earlier stage; the onter part of the rectus[1] described becomes gradually atrophied until the pectoralis major acquires its usual independent character. The above facts suggest that the pectoral muscles have been phylogenetically differentiated from the thoracic region of the rectus, their establishment taking place in connection with that of the sternum, which breaks up the uniformity of the latter muscle, primitively continuous from pubis to jaw. This conclusion is to some extent borne out by the condition observed in certain reptiles, where the distinction between the pars abdominalis pectoralis and the rectus lateralis has been attended with some difficulty[2]. Moreover, there exists in the Penguins

[1] This part of the muscle thins away posteriorly, and cannot be traced to the pubis; but we are not therefore entitled to deny it the character of rectus; for *cf.* the condition in some Reptiles (*Monitor* and *Lacerta*), where in the subcutaneous part of the muscle some of its fibres become attached to scales. *Vide* account of the Abdominal Muscles of Reptiles, by H. Gadow, Ph.D.

[2] For a full discussion of these muscles in Reptiles, see the same paper; which states that in *Ptyodactylus* the pars abdominalis pectoralis reaches as far as the third inscription of the rectus ventralis; but that in *Monitor*, *Lacerta*, and *Cnemidophorus* it is often found coalesced with the rectus lateralis.

(Spheniscidæ), partly overlying the pectoralis medius, a muscle described by Watson and named by him the Dermo-humeralis, which takes its rise from the head of the humerus, and forms in the abdominal region a thin band of longitudinal fibres lying near the median line: this is, in other words, a ventral part of the rectus continuous with a lateral part differentiated from the pectoralis. In these birds also the rectus is complex, consisting of two sheets (Watson *apud* Bronn).

B. *Middle sheet*, most massive of the three, and attached to the posterior-lateral borders of the sternum, which apparently corresponds with the rectus of other birds.

C. *Thin inner sheet*, which has the transversus attached to its edges. This takes attachment after passing *inside* the sternum for nearly one third the whole length of the latter. In the later stages its attachment travels backwards towards the end of the sternum, till in the embryo of 17 days it is completely united with the main body of the rectus, while the transversus has acquired its usual position with regard to the latter. This late ontogenetic change in the rectus seems to represent the posterior translation of the attachment of the rectus, during the late phylogenetic development of the long metasternum characteristic of this type, which apparently splits the muscle in two, and carries the upper part backwards as it grows.

3. In the earliest stage of the Guillemot, as in the Ostrich, there are seen transverse bands of muscle; these are afterwards lost, and fused into a uniform supercostal sheet continuous with the obliquus externus. This supercostal sheet eventually, in the latest stages examined, acquires attachment to individual ribs, while at the same time the obliquus externus acquires an attachment to the ribs and lateral borders of the sternum; the phylogenetic meaning of these changes is obvious.

4. There are indications of a slight posterior shortening of the costal sternum. There are 7 sternal ribs in the adult, but in the early embryo 9; of these the 7th, 8th, and 9th have no uncinate processes. Fig. I. (p. 690) shows an adult specimen in which the 9th rib is not only free at its sternal end, but atrophied also towards the dorsal region of its spinal parts. This mode of atrophy at both ends, which leaves a rudiment of the middle part of the rib, occurs again in the Chick. In the Ostrich, as has been seen, atrophy begins at or near the sternal end, and travels uniformly towards the spinal region. Neither in the Chick nor in the Ostrich do we find that marked division between spinal and sternal portions of the rib which in the case of the rudimentary 9th rib of the Guillemot divides it into two pieces.

The allied species, *U. brunnichii*, may be compared with this; the adult has also 7 sternal ribs, and 2 posterior ribs without uncinate processes, which do not reach the sternum.

There is also some indication of anterior shortening of the sternum, for one of the early embryos shows the attachment of a rib, which in the adult (*cf.* Plate XLIV. fig. 9) falls short of the sternum.

5. The metasternum is remarkable for the great reduction of the

lateral processes, and for a crescent-shaped ridge at the end. The former character is easily understood if we regard these processes as homologous with those of the Ratitæ, and consider the metasternum to have received special elongation at a late date. Plate XLIV. fig. 9 shows a condition which supports this view; the median part of the metasternum is here not longer than the process, while in the adult it is considerably longer; also the process is continued anteriorly into a ridge forming part of the undoubtedly costal sternum, which may be distinguished from the thinner cartilage of the metasternum adjoining it towards the median line.

The crescent-shaped ridge marks the posterior insertion of the pectoralis minor, which thus lies as it were in a depression of the sternum; this muscle is remarkable for its strength and its great elongation, taken in comparison with those of the pectoralis major.

(iii.) The Gull.

(11 specimens, from about 16 days' to 5 days' embryos.)

1. In several individuals of about 14 days there was traced a thin ventral portion of the rectus continuous with the pectoralis major.

2. Two specimens of about 11 or 12 days exhibited traces, consisting in greater thickness and greater strength of the fibres in the regions indicated, of a division of the rectus into three bands, a median, and two lateral attached to the posterior-lateral processes. In the adult the lateral part of the rectus is, on the contrary, very thin. The embryonic condition recalls that of the Ostrich; possibly the width of the sternum, which is somewhat broad for its length, may be associated with the early lateral thickness of the rectus.

3. The intercostales externi exhibit in the later stages the changes already described in the Guillemot; the supercostal sheet at the stage in which it is continuous sends a thin continuation under the pectoralis major, which passes over the sternum and is attached to it near the borders of the pectoralis minor.

A 5 days' embryo affords the clue to the intercostal nature of the primitive transverse bands seen in the previous types; bands precisely similar are seen alternating with and attached to the ribs, not overlying them as in the former cases; while part of their dorsal extent is already fused to form the continuous supercostal sheet referred to above. The connecting link between the supercostal and intercostal state of these bands is seen in the Chick, where the bands overlie the ribs, but where they are found on dissection to alternate with them in the cervical region.

4. The metasternum has two pairs of processes: of these the outer is identified as homologous with the posterior-lateral process in the Guillemot and Ostrich by the fact that its outer border affords the sternal attachment of the obliquus externus. The inner one is therefore of later origin; perhaps it owes its existence to the peculiarity of the posterior end of the pectoralis major, of which the lateral part is unusually strong and longer than the median, and is attached to

the edges of both processes. The second process is already indicated in the earliest embryos examined, so that it is clearly formed by addition, not by absorption. Plate XLIII. fig. 19, by the presence of the additional filling absent in the earlier embryos, shows an indication that the increased size of the pectoral muscles in birds that fly well demands increased breadth of their sternal attachments, and thus leads to the filling up of the sternum, so that the processes are obscured by their own growth, and finally become confluent.

5. In some, but not all, of the older specimens there was found a 7th sternal rib.

6. The condition of the anterior-lateral part of the sternum, which gives attachment to ribs anteriorly to the base of the coracoid, is to be contrasted on the one hand with the anterior-lateral process of the Ostrich, formed as a secondary addition to the rounded outline of the costal sternum, and on the other hand with that of the Chick, in which an apparent process of the costal sternum is first formed through the loss of two anterior ribs primitively attached and afterwards augmented by a secondary growth.

An old five days' embryo, the earliest examined, calls for a special description. The coracoid (*cf.* Plate XLIII. fig. 8) exhibits a remarkable resemblance to that of the Ostrich; the median depression, however, does not amount to a foramen, and it is filled by a separate mass of tissue, attached to the coracoid itself by embryonic muscular tissue. This specimen, which is quite normal and alike on both sides, seems to compel the conclusion that the coracoid of the adult Gull represents a fusion of the true coracoid with the precoracoid, in which the foramen which remains open in the case of the Ostrich is filled up by further ossification—a conclusion sufficiently startling, notwithstanding that so great an authority as Parker has already combated the assumption that the elements of the shoulder-girdle are the same in all birds. The scapula, as will be observed in the Chick at a similar age, is quite free from the coracoid.

This embryo presents a median mass of tissue, corresponding with the position of the top of the keel. The interpretation of this as an interclavicle is forbidden by the position of the clavicles, which are, as seen in the diagram, very small, far from the median line, and not even directed towards it; further, this centre, separated from the pericardial cavity only by the thinnest connective tissue, occupies a less superficial position than the clavicles, which overlie a thick stratum of embryonic muscle. It will be seen, on the other hand, that this centre arises in closest connection with the already approximated sternal halves. Comparison with a certain occasional median cartilage in the Chick will show that too much importance must not be attributed to this centre in the Gull; the former is also median, but its *posterior* position shows that it cannot be an interclavicle. It must therefore be a formation of recent date, and its occasional appearance shows that the keel has a *tendency*, not yet established, to differentiate itself from the rest of the sternum: this tendency is expressed, in a much lower degree, by the existence of a separate centre of ossification for the keel in the Gull and Chick, as in many

other birds. There is every reason to expect that this tendency will occasionally be expressed (as apparently it is in the present instance) by the thick anterior part of the keel, as well as by the posterior part.

(iv.) The Chick.

(37 embryos, from 16 days' to early 5 days'; of which all but 7 were under the age of 12 days.)

1. Continuity of the inner part of the pectoralis with outer fibres of the rectus was observed in Chicks of 7 days. At this age the part indicated cannot be strictly identified, but it seems to occupy the position of the pectoralis minor of the adult.

2. At the age of 6 days the condition of the rectus is peculiar. Its anterior part (the equivalent of the sterno-hyoid and genio-hyoid, of which only a few fibres have as yet been caught up by the hyoid bones) passes between the open clavicles to end in a wedge-shaped piece between the sternal halves, at a stage when the approximation of the latter has already cut the continuity of the primitive rectus band.

This state of the rectus and that described in the Guillemot warn us that embryonic conditions, when not comparable to those of any known adult form, cannot always be supposed to have a phylogenetic value. We can scarcely imagine that there ever existed a type in which, as in the Guillemot embryo, the rectus was attached to the clavicles, while the halves of a highly developed sternum, provided with processes, failed to meet in the middle line; or in which, as in the embryo chick, the presternal part of the rectus passed through open clavicles, while the sternum was closed.

3. The primitive bands of the intercostales externi are seen from the end of the fifth to the end of the sixth day. Their supercostal position seems to be due to the curvature of the ribs, each of these having passed forward under the intercostal muscle of the next; for in the cervical region, where several, usually three, are present anterior to the coracoid, complete dissection shows that they are, as in the case of the Gull, alternate with the rudimentary ribs of this part, although in the sternal region they are supercostal as in the Ostrich and Guillemot. The reason why no such alteration can be traced in the sternal region seems to be that the proximal ends of the bands thin gradually away in the region where the intercostales externi of the adult find their dorsal limit; in the neck region, on the contrary, they can at first be traced up to the spinal column, although at a later stage their spinal ends disappear. No bands were seen in the cervical region of the types previously described.

These bands on dissection are found to consist, at the end of the 6th day, of strong fibres at an angle with the direction of the band; distally these fibres form a blunt mass, so that the band has a round end, abruptly marked off from the thin undifferentiated muscle in which the bands lie.

The reasons for concluding that these bands represent (*a*) the

intercostales externi and (*b*) a primitive arrangement are the following:—

(*a*) (1). Their correspondence in number with the ribs, and intercostal position in the case of the Gull and Chick.
(2). Their subsequent fusion into a supercostal sheet, differentiated finally into the intercostales externi.
(*b*) (1). Their curvature, slight as compared with that of the ribs.
(2). Their extent beyond corresponding ribs, in the case of the cervical ribs of the Chick, and posterior ribs of the Chick and Ostrich.

It is to be hoped that further research may elucidate the origin and exact relations of these bands; the inquiry must be attended with some difficulty, however, since the mesoblast has but recently acquired histological differentiation when they present the appearances described.

4. The evidences of the shortening of the sternum are the following:—the adult condition presenting five ribs with uncinate processes and two long unattached ribs without them, one anterior and one posterior.

(*a*) *Anterior shortening.*

(i.) Chicks of 7 days showed in a number of cases the elongation of 1–3 ribs anterior to the first of those named above; none of these reach the sternum.

(ii.) Chicks early on the 6th day invariably showed two at least of these ribs fully attached to the sternum; they are very small and close together.

(iii.) The anterior muscle-bands, previously described, which atrophy from their spinal ends onwards, suggest that their corresponding ribs have passed into the sternum and disappeared by a process of atrophy like that already noticed in the Ostrich. This view is supported by the condition of a 5 days' Chick, which shows four of the muscular rudiments named overlying four minute masses of cartilage near the median line; this specimen is in many respects abnormal, but certainly these rudiments suggest the former existence of a pre-sternum.

(*b*) *Posterior shortening.*

In about one out of every four Chicks from 6 to 8 days incubated, there is a rudiment of a posterior 8th rib, atrophied at both ends as in the Guillemot; in earlier stages this rib is seen, but not so frequently, attached to the spinal end, or even at both ends. Before this rudiment disappears it approaches very close to the next rib, apparently because the intercostal muscle uniting them does not grow so fast as those elsewhere, and in one case the rudiment is seen attached to the next rib, forming a process (*cf.* Fig. III. diagr. *a*, p. 708). The 7th rib itself is often attached to the sternum up to the end of the 9th day.

The condition of the ribs in the ancestor of the Fowl, thus shown, may be compared with that of allied forms, the Waterhen and the

Rail. The posterior shortening is evidently of much more recent date than that just described at the anterior end.

5. There appeared indications of the compound character of the sternum. Several 5 days' Chicks, in which the pericardial cavity was not quite closed, exhibited, as already mentioned, thickenings alternate with the sternal ends of the ribs. Sowewhat later 5 days' Chicks showed (in that anterior part which by the end of the 5th day gives attachment to the coracoid) irregular thicker masses incompletely united.

If these traces of structure in the sternum appear somewhat slight to have any value assigned to them, it must be remembered that early on the 5th day *aggregation* of tissue is almost the only sign of differentiation of the mesoblast. Such aggregation is frequently seen better in dissections than in sections.

6. The posterior processes of the sternum are mapped out very early. In the Chick a newer process is added on the lateral aspect of the posterior-lateral process, whereas in the Gull one is added towards its median aspect. This process, the external xiphoid, appears in a 5 days' Chick as a minute outgrowth from the posterior-lateral process; its development may be traced by comparison of the diagrams.

Plate XLV. fig. 10 shows a 6 days' Chick with a sternum quite abnormal, in which two other processes appear. Possibly they may be formed as rudiments of the 7th and 8th ribs previously attached to the sternum; but the whole structure of this specimen is abnormal, especially in the following respects—(1) The position of the primitive intercostal bands, of which four lie ventral to the metasternum and nearly meet over it in the median line; (2) the condition of its coracoid aspect; and (3) the four rudiments in the neck, already described.

Finally, there remain to be discussed, 7, the *formation of the keel*, and 8, the evidences for or against the existence of an interclavicle.

7. In three Chicks out of the thirty younger specimens, there was found a separate cartilaginous centre for the keel. The ages of these three were 7 days. Two of the three centres are figured, to show that their posterior position precludes their being interpreted as interclavicles; the third was precisely similar; the clavicles at this stage are still open.

With these exceptions the keel was found to appear with the fusion of the halves of the sternum; these approach late on the 6th day and fuse gradually from the 9th till the beginning of the 10th day; as the fusion passes backwards, so does the keel. It is at first low, but afterwards acquires its full height. These facts, taken in connection with that long ago established by L'Herminier, that ossification of the keel commences at its base (where the keel is not, as in the Duck and Heron he states it to be, ossified by fusion of paired centres in the sternum), point to the conclusion that the keel is a structure formed by the fused edges of the halves of the sternum. Its centre of ossification is, according to the same authority, the last to appear in the sternum of the Chick. Götte's account of the

formation of the Chick's keel is, however, as follows:—*Stage* 1: at an age when both sternum and clavicles are cartilaginous, they are united by a tissue, which at the age of 5 days is comparatively thin and dim, but between 4 and 5 days is dark. *Stage* 2: subsequently, but still prior to the closure of the sternal halves, this tissue looks like a projection continuous with the sternum. *Stage* 3: the cartilaginous borders of the episternal region of the clavicles meet to form the keel: at what date this takes place he does not make clear, but it must be either during, or prior to, the latest stage he describes, viz. the 8 days' Chick, in which he considers the median broadening of the tract of commencing ossification in the furcula to represent the ossifying interclavicle.

Now in the specimen examined the said dim and thin tissue between the clavicles and sternum was never observed to present such an appearance as that described in Stage 2; but it was differentiated, immediately on the complete differentiation of the mesoblast, into muscular fibres, forming a tract that gradually narrowed as the clavicles closed. During the closure of the sternum it becomes reduced to a thin string; and all muscular fibres having now disappeared from it, it assumes its character as the sterno-clavicular ligament of the adult. No indication was observed tending to show that its origin differed from that of other ligaments contemporaneously established, such as those of the wing; nor was there seen any stage in which the cartilaginous borders of the so-called episternal region of the furcula approached the keel; they were always separated from it by this tract, first consisting of embryonic muscular fibres, and afterwards of thin ligament.

8. So much with regard to the development of the keel; if we accept the view that it is an apophysis of the sternum, established for the attachment of the pectoral muscles, we have none the less, however, to examine the evidence as to the existence of an interclavicle. That the furcula presents a median prolongation, is undeniable; but the following statements on two points will show reasons for supposing it to be an outgrowth derived from the clavicles only at a late date.

(1) *Date of the formation of the so-called Interclavicle.*—It is somewhat difficult to ascertain the exact age of Chicks later than the 5th day of incubation, because the changes they undergo are comparatively slight; but we may recall the fact that the two anterior ribs lose their attachment to the sternum about the end of the 6th day, while the occasional free rudiment of a rib eighth from the first long one of the adult is never seen later than the 8th day. In other words, the ribs at any rate have established their *generic* characters at this date, which renders it probable that the broadening ossification of the median region of the clavicles, described by Götte as established during the 8th day, is an outgrowth of the Avian furcula rather than a pre-Avian interclavicle—a view which is expressed by giving to it (as has been done throughout this paper) the name of *median furcular apophysis* rather than of *interclavicle*.

(2) *Position of parts in the Shoulder-girdle of the 5 days' Chick.*—

It is always stated that the coracoid and scapula of the Chick arise as a single plate, but the various specimens examined did not bear out this description. The shoulder-girdle of the 5 days' chick, in which the pericardial cavity is not quite closed, is shown in figs. 4 and 5, Plate XLIV. It consists of three pieces, whereof the middle one is partly attached to that nearest the median line. According to Götte, who maintains the usual view that the scapula and coracoid form a single plate, and who further describes the episternal projection of a 5 days' Chick as clearly distinguishable from the clavicle itself, these three pieces would be interpreted as coraco-scapular plate, clavicle, and interclavicle; but this interpretation, rendered doubtful by the early separation of scapula and coracoid, already noticed in the Ostrich and the Gull, is rendered impossible by comparison of subsequent stages. Plate XLIV. figs. 3, 4, 5, and 6, show how the median piece gradually elongates, without growing thicker, and forms the clavicle, while the intermediate and the dorsal piece fuse to form the coraco-scapular mass usually described, which was found to exist early on the 6th day (fig. 6). The late date of its appearance suggests that this fusion may represent rather a Struthionic than a pre-Avian condition.

The interpretation as clavicle of the median piece which is partially attached to the intermediate one, agrees with the description of Rathke, who says that at an early stage the coracoid and clavicle are united dorsally but not ventrally; nor is it inconsistent with that of Götte himself, who says the end of the coracoid passes under the clavicle, which is the same thing in other words. Now the median piece, though posteriorly free, is united anteriorly to the coracoid; and this anterior union is *dorsal*, for the two pieces appear separated by a crack when seen from the surface (*cf.* figs. 3 and 4), yet on dissection they are found united below.

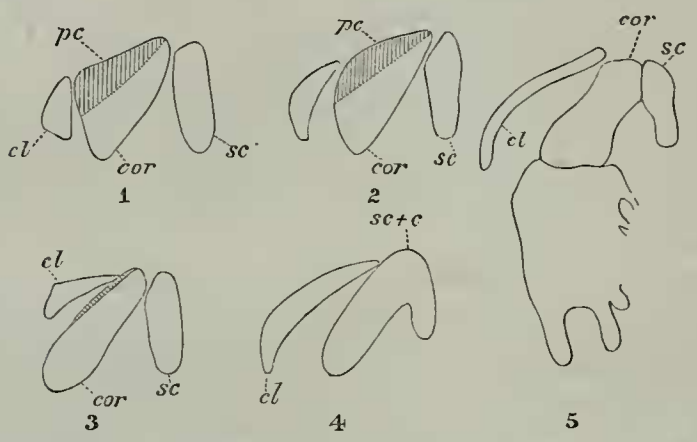
At first sight the relative positions of the two pieces present a difficulty in the interpretation just given, viz., that they are placed end to end, not parallel as in the adult, so that the clavicle is separated from the scapula by the whole length of the coracoid. The same difficulty, however, attends Götte's account of the relation of the two parts; since, although he traced the end of the coracoid under the outer end of the clavicle, he expressly states that he failed to trace it far towards the median part of the clavicle; in other words, he also found the two placed, at this stage, end to end.

Again, a second difficulty lies in the fact that the intermediate piece of the shoulder-girdle is triangular, which the coracoid is not. During the 5th day, however, it loses this triangular shape, and is no longer found to be, as at first, a flat mass, comparatively thin. This change suggests that possibly the anterior apex of the triangle is equivalent to the precoracoid of the 5 days' Gull (which also forms a mass lying between the clavicle and scapula), and that the clavicle is gradually carried up towards the dorsal end, by the atrophy of that part, with which it is in close connection. This theory is best explained by the following series of diagrams. Reference to the Plates will show that, although themselves diagrammatic, these figures

correspond exactly with those drawn from actual specimens in different stages (see Plate XLIV.).

It is to be clearly understood that the broadening median end of the clavicle, which Götte describes in its condition during the 8th day of incubation, and interprets as an interclavicle, has nothing to do with the broad median end of the triangular clavicle figured below. The clavicle becomes uniformly thin throughout its length toward the close of the 6th day, as shown in diagram 3, fig. II.

Fig. II.



1, 2, 3, show changes in the shoulder-girdle of the Chick, late on the 5th day of incubation; 4, shows its condition during the 6th day; and 5, its condition late on the 6th day, when the coracoid bone has acquired its sternal attachment and the coracoid and scapula have almost separated.

The view above suggested with regard to the presence of a rudimentary precoracoid in the Chick at a early stage, is borne out by comparison of the condition of the internal part of the coracoid in various types.

Beginning with the Ratitæ, we see that where the precoracoid is apparently lost, there seems to be a rudiment of it remaining in the form of a process of the coracoid, situated in *Dromæus* (Plate XLIV. figs. 15 and 16) just beneath the clavicle. In *Casuarius* it seems possible that the area of bone extending internally to the *foramen* or *incisura coracoidea*[1] is also comparable with the precoracoid, since in *Struthio* the said foramen is situated near the internal margin of the bone; but whether this precoracoid area is not rather a new growth of the coracoid than the homologue of the Struthionic precoracoid, is very uncertain. The peculiar marginal foramen seen in Plate XLIV. fig. 7 is seen partly developed, occasionally, in the Ostrich, where the precoracoid is present—a fact which supports the

[1] This gives a passage to one of the nervi brachiales inferiores; this nerve supplies the m. supracoracoideus (called pectoralis minor elsewhere throughout this paper).

former view rather than the latter. Even in *Casuarius* it is only occasional (*cf.* fig. 8).

The same uncertainty must exist with regard to the precoracoid of *Diomedea* (fig. 1, Plate XLIV.); although there can be little doubt, from comparison with the early stages of the various embryos figured, that we must agree with Sabatier in regarding this region as the Avian precoracoid, rather than the precoracoid of Parker, which Sabatier calls an epiphysis (*cor. ep.*, fig. 1).

Under these circumstances it would be hazardous, notwithstanding the Struthionic aspect of the coracoid in the Gull, to put forth with any certainty a view that the pre-Avian kind of precoracoid is to be identified with the region suggested as precoracoid in the Chick; but at the same time the development of this marginal region in the types figured renders it extremely likely that the region already described in the shoulder-girdle of the late five days' Chick is equivalent to a precoracoid of some kind, though possibly of a secondary character, developed in the more immediate ancestors of the Gallinaceæ.

(v.) The Gannet.

(9 specimens, from the bird just hatched to a stage comparable with a 5 days' Chick.)

The sternum of the adult Gannet, it may be observed, since it possesses a furcula continuous with the keel, and behind it a median paired apophysis for the support of ligaments, exhibits at once the interclavicle of Götte in front, and the interclavicle of Harting at a more dorsal level.

In this bird, if in any, we might expect to trace a genetic connection between clavicle and keel, since in the adult these parts are fused. Such, however, is not the case.

The embryo is particularly easy to examine, because it is so large that the earliest aggregations in the mesoblast can be clearly traced. The following were the stages observed, recorded, for the sake of convenience, in inverse order, youngest first.

1st Stage, corresponding with a five days' Chick.—There are 8 ribs, which end freely, and no trace of sternum. The three parts of the shoulder-girdle are separate and almost parallel, overlying a remarkably thick mass of tissue representing the pectoral muscle.

2nd Stage, corresponding with a later five days' Chick.—The sternum is indicated by thick opaque aggregations in a layer of mesoblast, shown in fig. 14, Plate XLV. A large mass indicates the sternum, a smaller one the keel, while three smaller masses, which in the next stage have disappeared, may probably be compared with the three anterior muscle-bands previously described in the Chick. The end of the clavicle, which is of course superficial, lying next to the skin, is completely shut off from the deeper layer, in which lie the differentiating sternum and keel, by the whole thickness of the pectoral muscle, a depth nearly half the length of the clavicle itself.

3rd Stage, corresponding with a six days' Chick.—This shows

the sternum fully formed, lying in a position corresponding with that of the masses just described, and fused with the rib. The keel exists as a broad and thick longitudinal ridge, divided from the body of the sternum by a deep groove on the dorsal side. The coracoid has now acquired attachment to the sternum; the clavicle is still shut off from the sternum by the pectoral muscle. The scapula does not join the coracoid to form a coraco-scapular plate, either at this or any other stage. A rudiment is apparent of the ligament joining the top of the coracoid with the top of the keel; and a very strong rudimentary ligament, reduced in later stages, unites the top of the scapula with the top of the keel. The anterior-lateral process is very thin and trilobed, which perhaps indicates an origin from three anterior ribs belonging to the three anterior muscle-bands indicated in the last stage. There are 7 sternal ribs.

The outline of the fore limb at this stage indicates a division into three digits; it is shown in Plate XLIII. fig. 4 *a*, for comparison with the fore limb of the 7 days' Ostrich.

4th Stage, corresponding with a Chick of about 12 *days' incubation.*—The lateral halves of the sternum are closed, the keel is fully formed, and the pectoral muscle has acquired the adult structure, namely, of three interconnected sheets. The clavicle is united to the keel, but dorsally a thin crack still indicates their junction (fig. 16, Plate XLV.). The anterior-lateral process of the last stage has been atrophied; this fact may be compared with that of the loss of the two anterior ribs at a subsequent stage. On the right side is seen the peculiar insertion of the coracoid characteristic of the adult.

The posterior-lateral process of the metasternum has been added. No *posterior* reduction of the ribs is to be traced. In fact the posterior part of the sternum seems to retain what we may suppose to be a primitive type, as will be seen on comparison of the successive stages (figs. 15, 17, 18, Plate XLV.) with those of the Ostrich (figs. 3, 4, and 5, Plate XLII.). We may contrast these with the condition of the metasternum of the Chick, doubtless a form highly specialized in this respect as in many others; in it, as we have seen, the processes of the metasternum are established from the first.

5th Stage, corresponding to a 14 *days' Chick.*—This shows the addition of the median process of the metasternum. The double apophysis of the median and anterior region is not added till a later stage. In the Chick, the median anterior apophysis is added between the end of the 9th and the beginning of the 14th day of incubation.

Part III. Conclusions drawn from the above data,

in connection with facts previously known.

1. Conclusion drawn from the existence in the embryo of anterior ribs atrophied in the adult, of which some are seen attached to the sternum, and of muscle-bands apparently representing the intercostales

externi of these ribs[1]:—*that the sternum of birds has undergone an anterior shortening*, consequent on that posterior translation of the shoulder-girdle which is at once expressed by the lengthening of the neck and the shortening of the trunk in the Avian as compared with the Reptilian type; owing to this change of place, the front part of the sternum has been severed from the ribs that formed it, so that these are now atrophied, and only traced in the embryo.

It can scarcely be doubted that the manubrium sterni of mammals owes its origin to ribs lost in a similar shortening of the trunk, by which the seven constant vertebræ of the mammalian type established their cervical character, ribs which are still present in the Monotremes. The part of the Avian sternum called by Huxley the "manubrium" or "rostrum" has, however, nothing in common with the manubrium sterni of mammals; it is a secondary outgrowth formed for the attachment of the sterno-clavicular ligaments. The anterior portion of the sternum of the *Ostrich*, however, is truly a kind of manubrium; it projects anteriorly between the attachments of the coracoids, and, as is seen in the diagram (Plate XLII. fig. 3), it projects far in front of the first sternal rib.

2. Conclusion from the atrophy observed to take place of one or two posterior ribs, and the addition of the median and posterior part seen to take place in the embryo of the Ostrich:—that the posterior shortening of the sternum suggested by Gegenbaur is but slight, varying in different types; and that it is far more than compensated by the addition of the long metasternum.

3. Conclusion from the development observed, in connection with changes in the muscles:—

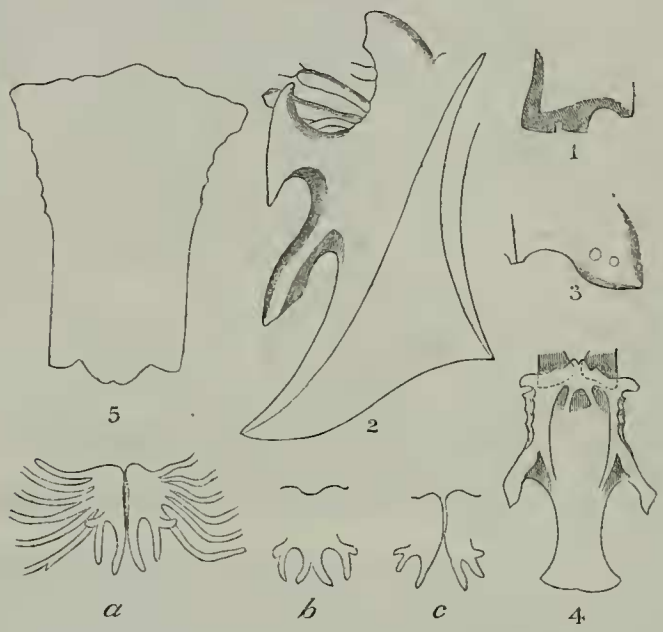
That the posterior lateral processes, though primitively representing the ends of the costal bands, are elongated and modified in various types according to the exigencies of mechanical strain. For this reason they are never found in connection with posterior ribs that suffer atrophy, as might at first sight have been expected from comparison of the costal processes of the sternum of *Iguana*.

The great variation in form of the processes leads us to look for some modifying cause that varies in the types to which they belong. Now since the posterior border of the sternum affords attachment to two opposite sets of muscles, (*a*) the pectoral, (*b*) the abdominal, the resultant of their forces must be to some extent expressed in its shape, for in general the outline of a bone tends to express the direction and strength of the mechanical forces acting on it. In other words, we should expect to find the posterior border of the sternum varying with the habits of the bird, whether it is a good flyer, and uses its pectoral muscles most, or is accustomed to run or hop, and thus makes a greater proportional use of its abdominal muscles. This is exactly what takes place: in birds of great power of flight the processes become long, broad, and finally confluent, so that a long

[1] It is understood that the m. longus lateralis cervicis (Gadow, Bronn, Vögel, p. 117), *i. e.* m. longus colli externus of Watson, seen in the Spheniscidæ (*op. cit.* p. 61), is a continuation and serial homologue of the mm. intertransversarii and intercostales externi.

sternum, plain in outline, is produced; in birds that hop and run more than they fly, long, thin processes are seen for the attachment of certain abdominal muscles, but the rest of the sternum is not filled up, so that we have a very short sternum with complicated processes. In proof of this, contrast the sternum of the Gull, in which the two pairs of lateral processes, which afford attachment to the end of the

Fig. III.



1, 2, 3, posterior outline of the sternum in *Procellaria gigantea*, *Diomedea exulans*, and *Crax alberti*; the shaded part is very thin, and the presence of a similar thin margin on the flattened ribs of the last-named conclusively shows that this margin results from a process of addition. 4, sternum of *Didunculus*, 5, of *Hesperornis* (cast), showing posterior lateral process; the last shows, like *Casuarius*, *Rhea*, and fig. 9, Plate XLII., an incomplete fusion, probably due to the same causes that have operated in widening the sternum during the establishment of the Avian type. (All C.C., reduced.)

a, *b*, *c*, sterna of 8 and 9 days' Chicks: *a*, shows abnormal persistence on the right side of rudimentary 8th rib attached to the 7th; *b* and *c*, dorsal and ventral aspects of sternum, showing incomplete keel and absence of median furcular apophysis.

large pectoralis major, are scarcely seen to project from the sternum, with the sternum of the Fowl or Tinamus, in which the long processes afford attachment merely to a few thin fibres of that muscle. Sterna of the Common Duck show much variation, with a tendency to fill up the sternum. The sternum of the Gull (*cf.* Plate XLIII. figs. 9 and 10) shows how the process of filling up takes place. In all the specimens examined except the one figured, the two processes were distinct, even in the earliest stages examined;